Morphology and life history of the Great Slave Lake ciscoes (*Salmoniformes: Coregoninae*)

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January 2014

Canada

Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research documents are produced in the official language in which they are provided to the Secretariat.

Correct citation for this publication:

Muir, A.M., Vecsei, P., Power, M., Krueger, C.C., and Reist, J.D. 2014. Morphology and life history of the Great Slave Lake ciscoes (*Salmoniformes: Coregoninae*). DFO Can. Sci. Advis. Sec. Res. Doc. 2013/047. v + 29 p.

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ABSTRACT

The ciscoes (*Salmoniformes: Coregoninae*) have radiated into complexes of closely related species, life history types, and ecological variants. The taxonomy of the North American ciscoes remains unresolved. We provide the first comprehensive description of the Great Slave Lake ciscoes by comparing gross body morphology, phenotypic and life history traits, and habitat use among morphs, and assessing the validity of morphs within the context of existing taxonomy. At a minimum, our analysis supports the hypothesis that the Great Slave Lake ciscoes include two strongly differentiated species (*Coregonus artedi* and *C. sardinella*) and an adfluvial *C. artedi* morph that is distinct from its lacustrine conspecific in terms of life history, morphology, age, growth, and mortality. *C. sardinella* has previously been identified from Great Slave Lake, but we provide the first comprehensive description of this species in the lake and confirm a significant range extension for the species. The lacustrine *C. artedi* differs little from descriptions throughout its range. In addition to these three ciscoes, linear phenotypic traits, gillraker number and morphology, and growth data support the possible occurrence of two other, less-distinct morphs, the big-eye cisco *C. artedi* and *C. zenithicus*. Although the big-eye morph was not identified by cluster analysis of body shape and linear phenotypic measures, it was visually identified on the basis of differences in traditional phenotypic proportions, such as eye diameter, paired fin lengths, and head and gillraker morphology expressed as thousands of standard length. In addition, the big-eye morph showed different age and growth structure compared to the other lacustrine cisco morphs. *C. zenithicus* was distinguished visually and by the statistical model of linear phenotypic traits as well as by gillraker number and morphology, which were within the range for the species across its distribution. Identifying, characterizing, and managing locally-adapted cisco morphs that reflect important ecological and bioenergetic linkages is critical to conserving the ecological integrity of northern ecosystems.

**Morphologie et cycle biologique des ciscos du Grand lac des Esclaves
(*Salmoniformes : corégoninés*)**

RÉSUMÉ

Les ciscos (*salmoniformes : corégoninés*) se sont répandus en complexes d'espèces, en types de cycles biologiques et en variantes écologiques étroitement liés. La taxonomie des ciscos de l'Amérique du Nord demeure méconnue. Nous donnons la première description exhaustive des ciscos du Grand lac des Esclaves en comparant de façon générale la morphologie corporelle, les caractéristiques du phénotype et du cycle biologique ainsi que l'utilisation de l'habitat parmi les formes, et en évaluant la validité des formes dans le contexte de la taxonomie actuelle. Au minimum, notre analyse appuie l'hypothèse selon laquelle les ciscos du Grand lac des Esclaves comptent deux espèces fortement différentes (*Coregonus artedi* et *C. sardinella*) ainsi qu'une forme adfluviale de *C. artedi* qui se distingue de son congénère lacustre par son cycle biologique, sa longévité, sa croissance et sa mortalité. *C. sardinella* a déjà été identifié dans le Grand lac des Esclaves, mais nous fournissons la première description complète de cette espèce dans le lac et confirmons une augmentation importante de l'aire de répartition de l'espèce. La description de la forme lacustre de *C. artedi* varie légèrement dans l'ensemble de son aire de répartition. En plus de ces trois ciscos, des données sur les caractéristiques linéaires du phénotype, le nombre de branchiospines, la morphologie et la croissance soutiennent l'hypothèse de la cooccurrence de deux autres formes moins différentes, une variante de *C. artedi* (« big-eye ») et le cisco à mâchoires égales (*C. zenithicus*). Bien que la forme « big-eye » n'ait pas été identifiée par une analyse de concentration des mesures linéaires du phénotype et de formes du corps, elle a été visuellement identifiée grâce aux différences dans les proportions traditionnelles des phénotypes, comme le diamètre des yeux, la longueur des nageoires paires, et la morphologie de la tête et des branchiospines, exprimées en milliers, par rapport à la longueur standard. De plus, la forme « big-eye » affichait différentes structures selon l'âge et la croissance par rapport aux autres formes lacustres de ciscos. *C. zenithicus* pouvait être distingué visuellement et à l'aide du modèle statistique des caractéristiques linéaires du phénotype ainsi que par son nombre de branchiospines et sa morphologie, qui correspondaient à la fourchette de mesures pour l'espèce dans l'ensemble de son aire de répartition. Il est essentiel d'identifier, de caractériser et de gérer les formes de ciscos adaptés à l'échelle locale qui reflètent d'importants liens écologiques et bioénergétiques afin de conserver l'intégrité écologique des écosystèmes nordiques.

INTRODUCTION

The ciscoes (Salmoniformes: Coregoninae) have radiated into complexes of closely related species, life history types, and ecological variants throughout their Holarctic distribution (Bernatchez 2004; McPhail and Lindsey 1970; Schluter 1996). Weak genetic differentiation, incomplete reproductive isolation, and strong plastic responses to environmental gradients make taxonomic classification of coregonines challenging; therefore, the taxonomy and evolutionary history of North American ciscoes remains unresolved.

A further complication to resolving North American cisco taxonomy is that commercial exploitation, local extirpation (Phillips and Ehlinger 1995), and hybridization and introgression (Todd and Smith 1992; Todd and Stedman 1989) have acted to reduce diversity in this group of fishes. With the exception of Great Bear and Great Slave lakes, NT, cisco diversity has been altered or replaced by non-native planktivores in all of the North American Great Lakes. Great Slave Lake (61°47'N; 113°43'W) contains an intact assemblage of post-glacial fishes, including ciscoes, and offers the opportunity to study this diversity in a relatively unperturbed ecosystem. In this sense, Great Slave Lake serves as a model to understand the historical post-glacial structuring of the native food web of the Laurentian Great Lakes and may provide insights and expectations to help guide restoration efforts in these systems (Zimmerman and Krueger 2009).

Our ultimate goal is to understand patterns of cisco diversity within and among North American large lakes and the biotic and abiotic processes shaping that diversity. A first step towards that goal is describing the patterns of cisco diversity in Great Slave Lake (Figure 1). A recent preliminary survey (Vecsei et al. 2012) identified five ciscoes including: 1) a large morph of *C. artedi* with a lacustrine life history; 2) a small morph of *C. artedi* with a lacustrine life history; 3) a 'dwarf' *C. artedi* with an adfluvial life history; 4) *C. zenithicus*; and 5) *C. sardinella*. The two lacustrine *C. artedi* (groups 1 and 2 above) were shown to be synonymous by Muir et al. (2013), who reported young lacustrine *C. artedi* underwent ontogenetic shifts in gillraker and body morphology and habitat use. The lacustrine *C. artedi* group was also sub-divided into the typical lacustrine *C. artedi* and a deepwater variant (the big-eye cisco; Muir et al. 2011). Strong phenotypic variation between the lacustrine and adfluvial *C. artedi* morphs was shown to reflect adaptations to their contrasting life histories and habitats (Blackie et al. 2012). In addition, the group identified as *C. sardinella* by Vecsei et al. (2012) was recently confirmed as such using amplified fragment length polymorphism (AFLP; J. Turgeon, Université Laval, pers. comm.). On the basis of these previous studies, five cisco taxa were thought to occur in Great Slave Lake including three species (i.e., *C. artedi*, *C. sardinella*, and *C. zenithicus*) and two morphs (i.e., adfluvial *C. artedi* and the deepwater big-eye cisco variant).

The purpose of this study is to provide an updated and more complete description of Great Slave Lake cisco morphs and their life history using new knowledge and an expanded sample size. Our specific objectives were as follows: 1) compare gross body morphology and phenotypic traits among morphs; 2) compare life history dynamics among morphs; 3) compare physical resource use among morphs; and 4) assess the validity of morphs within the context of the most recent taxonomy (Scott and Crossman 1973). Achieving these objectives will facilitate follow-on comparative studies among perturbed and unperturbed lakes to test predictions about the processes generating and maintaining ecological diversity and studies of the functional diversity among cisco morphs.

METHODS

Study site—Four lacustrine sites and one riverine site in Yellowknife Bay and two lacustrine sites and one riverine site in the east arm of Great Slave Lake (61°N, 113°W) were sampled

during fall 2008–2010 (Figure 1; Table 1). Sites were selected to span the range of available cisco habitat: 0–29 m, 30–59 m, 60–89 m, >90 m based on local knowledge and bathymetry.

Fish collections—Fish were caught in the lake using <24 hour, bottom set, multi-mesh gillnets. Nets were 200-m long x 1.8-m deep and composed of eight 25-m panels of 12.7-, 25.4-, 38.1-, 50.8-, 63.5-, 76.2-, 88.9-, and 101.6-mm stretch mesh. Fish were caught in the two rivers using a dipnet.

Statistical methods—Statistical analyses (significance level was set at $\alpha=0.05$) were conducted using R (2.15.1; R Core Team 2012), SigmaPlot 11 (Systat Software Inc., San Jose, California), the Thin Plate Spline software suite (TPS; State University of New York at Stony Brook, and MCLUST V.3 implemented in R (University of Washington). Non-parametric tests were used when data could not be transformed to meet the assumptions of parametric methods (Hollander and Wolfe 1999).

Morphology—Gross body shape of each individual was quantified using geometric morphometric methods (Bookstein 1989; Rohlf and Bookstein 2003; Zelditch et al. 2004). A calibrated digital image of the left side of each individual was captured according to Muir et al. (2012). Sixteen homologous (landmarks 1–16; Figure 2) and four semi-sliding landmarks (landmarks 17–20; Figure 2) were digitized on images using TPS and following Muir et al. (2013). Briefly, landmark data were used to scale each individual relative to a consensus form using TPSrelw. The 36 partial warp scores (i.e., size–independent shape) were entered into an ordination and the first two principal components (PCs) were retained as new shape variates and used in subsequent analyses (see Zimmerman et al. 2009).

Body shape was compared among morphs using a Bayesian cluster analysis, which does not require *a priori* assignments of individuals to groups (i.e., MCLUST; Fraley and Raftery 2009). Two MCLUST models (EII and VII see Fraley and Raftery 2009 for model descriptions) were fit to the body shape data (i.e., PCs 1-2 from an ordination of partial warps) and the 'best' model representing the most likely number of groups was identified using Bayesian Information Criterion (BIC). The 'best' or maximum-BIC model assigned individuals to groups and quantified uncertainty in group membership. Alternative candidate models were evaluated by BIC differences—the difference for the ith model was calculated as $\Delta BIC_i = BIC_i - BIC_{min}$, where BIC_{min} was the smallest BIC value among all candidate models (Burnham and Anderson 2002; Posada and Buckley 2004). Evidence supporting model i was considered strong if $\Delta BIC_i >150$ (Posada and Buckley 2004).

Traditional phenotypic traits were also quantified for each individual fish. Twenty-three linear morphometric measures (Table 2) and nine meristic characteristics (Table 3) were quantified on thawed specimens according to Koelz (1929), Scott (1960), and Vuorinen et al. (1993). Linear measurements were made on the left side of the fish using a digital caliper (± 0.01 mm). The first left gill arch was extracted, fixed in 5% formalin, and transferred to 95% ethanol prior to gillraker enumeration.

Linear phenotypic measures were treated in a process that paralleled the analysis of geometric shape data. Due to strong correlations with body size, all linear measures were size-adjusted using common-within-group residuals (Reist 1985, 1987). A subset of morphometric characters (OOL, PSL, IOW, GRL, and CPL; see Tables 2 and 3) that are known to vary among cisco morphs (see Koelz 1929; Clarke 1973) were identified and used to assess group structure. The first two principal components from an ordination of the size-corrected, linear phenotypic measures were retained as new variates and used in subsequent analyses. Scores on the first two PCs were analyzed by MCLUST according to the methods described above for the body shape data. The best model was selected by BIC and used to assign individuals to groups.

With the exception of gillraker number, most meristic characters were minimally informative in characterizing groups (i.e., low among group variation); therefore, these data were omitted from further analyses and used for descriptive purposes only. Gillraker distribution was compared among morphs because gillraker number is traditionally used as a primary trait for differentiating among coregonine taxa (Scott and Crossman 1973; Smith and Todd 1992; Todd and Smith 1992). A Kruskal-Wallis one-way analysis of variance (ANOVA) on ranks tested for differences in gillraker distributions among cisco morphs and Dunn's Test was used for all pairwise comparisons due to unequal sample sizes.

Life history— Fish age was estimated using a crack-and-burn method (Muir et al. 2013). A Kruskal-Wallis one-way ANOVA on ranks tested for differences in age distributions among cisco morphs and Dunn's Test was used for all pairwise comparisons due to unequal sample sizes.

Growth of cisco morphs was quantified by fitting a series of von Bertalanffy models to length-at-age data (Ogle 2012). The original model parameterization was used:

$$E [L \mid t] = L_\infty - (L_\infty - L_0)e^{-Kt} + \varepsilon,$$

where the expected standard length (*L*) at time (*t*) is a function of the asymptotic mean length (L_∞; theoretical mean length to which a fish would grow if time permitted), the mean length at time zero (L_0; i.e., hatch), and the growth coefficient (K y^{-1}; i.e., instantaneous rate at which *L* approaches L_∞), plus additive error (ε) (von Bertalanffy 1938). Age-0 and age-1 juveniles were underrepresented in the samples; therefore, L_0 was fixed to the measured mean length at hatch (i.e., 10.69 mm) for laboratory-reared Lake Superior *C. artedi* (Oyadomari and Auer 2007). Annual growth rate (ω) was estimated by $L_\infty * K$ (mm·y^{-1}; Gallucci and Quinn 1979).

Four nested models were fit to length-at-age data to compare growth among morphs: 1) *General*: separate parameter estimates for each morph; 2) *Common L_∞*: constant L_∞ among morphs, but varying K; 3) *Common K*: constant K, but varying L_∞; and 4) *Common*: the same parameter estimates for all morphs combined. The "best" model was selected by AIC (Akaike 1973) and a likelihood ratio (Bates and Watts 1998) tested the best model against the *Common* model (i.e., one growth curve for all morphs combined).

Survival (*S*) was calculated for the adfluvial and lacustrine *C. artedi* morphs, and for *C. zenithicus* as: e^{-Z}, where the instantaneous total mortality (*Z*) was estimated for each morph by the slope of a linear regression through the descending limb of an otolith-based catch curve (Ricker 1975). Small sample sizes within many of the older age classes prevented the calculation of *S* for the big-eye cisco and *C. sardinella*. An *F*-test for the equality of regression slopes was used to detect differences in *S* among morphs (Zar 1999).

Physical resource use—Minimum and maximum water depths (m) were recorded for each sampling event using an echo sounder. A Kruskal-Wallis one-way ANOVA on ranks tested for differences in depth-of-capture between cisco groups. Dunn's Test was used for all pairwise comparisons. Catch per-unit-effort (CPUE) was standardized to kg of fish·net^{-1}·24 h^{-1} and considered a relative index of abundance among depth strata. A Kruskal-Wallis with Dunn's comparisons tested for differences in CPUE among morphs within depth strata (0–29; 30–59; 60–89; >90 m).

Buoyancy was used as one physiological indicator of habitat and prey use. Percent buoyancy accounts for differences in soft and hard tissues that affect the specific gravity of the fish (Alexander 1972) and is negatively correlated with body lipid content and depth-of-capture in many fishes (Zimmerman et al. 2006). Low percent buoyancy (i.e., high body lipid content) is a more energy-efficient buoyancy control adaptation than the swim bladder for facilitating vertical migration in deepwater fishes (Alexander 1972, 1993). Many Great Lakes ciscoes undergo diel vertical migration to prey on *Mysis diluviana* (hereafter *Mysis*); low percent buoyancy is

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indicative of this behaviour (Clemens and Stevens 2003; Eshenroder et al. 1998). Percent buoyancy was calculated as follows: (weight of fish in water/weight in air)*100 (Krause et al. 2002; Zimmerman et al. 2006), where whole body weight (± 1 g) was measured using a Pesola spring scale (Jennings 1989). To measure weight of the fish in water, an incision was made on the left side of the fish, just below the lateral line, and extending from the anterior to the posterior of the gut cavity. The swimbladder was punctured; care was taken not to damage the internal organs. Once the fish was suspended in water, the remaining air was forced out of the swimbladder and gut cavity so that it did not bias the measurement.

An ANCOVA with L_s as the covariate tested for differences in buoyancy among cisco morphs. This analysis was restricted to fish with water weight > 2 g due to inaccuracies in measuring weights < 2 g with spring scales. The interaction term was included to test for homogeneity of slopes. A lack of homogeneity of slopes necessitated a size-correction; therefore, percent buoyancies were adjusted using a regression technique where residuals from the relationship between percent buoyancy and L_s for each of the five morphological groups were retained as new variates (Reist 1985). Residual percent buoyancies were compared among groups using a Kruskal-Wallis one-way ANOVA on ranks with Dunn's method of multiple comparisons.

RESULTS

Morphology—Three groups were identified on the basis of geometric body shape (Figure 3; MCLUST; ΔBIC = 259). Four of the five next best models also identified three groups (254 ≤ ΔBIC ≥ 243), indicating strong support for three geometric body shape groups. Two of the three groups identified by the model conformed to our field taxonomic assignments as well as groups previously identified by Vecsei et al. (2012). One of these groups consisted of 99% of fish identified as adfluvial *C. artedi* in the field and the second group consisted of 93% of fish identified as *C. sardinella* in the field (Figure 3). The third group identified by geometric body shape contained the greatest number of specimens and the most variation along both PC1 and PC2. This group contained specimens that were identified in the field as lacustrine *C. artedi*, big-eye cisco, and *C. zenithicus*. The body-shape group structure identified by the model was consistent with our expectation based on field and laboratory observations that adfluvial *C. artedi* and *C. sardinella* could easily be identified on the basis of body shape alone.

In contrast to the body shape model, four groups were identified on the basis of the selected linear phenotypic measures (Figure 4; MCLUST; ΔBIC = 1.60). The next best model, which was virtually identical to the first, also identified four subgroups on the basis of the selected linear phenotypic measures. All four groups were consistent with groups previously identified by Vecsei et al. (2012). Groups 1–4 consisted of 80%, 65%, 77%, and 97% of fish identified in the field as adfluvial *C. artedi*, *C. zenithicus*, lacustrine *C. artedi*, and *C. sardinella*, respectively. The selected linear morphometric measures were insufficient to separate the big-eye *C. artedi* morph— 97% of big-eye cisco were grouped with the adfluvial *C. artedi* contrary to our expectation that they would group with lacustrine *C. artedi*.

Gillraker number, a character typically used to differentiate coregonine ciscoes, differed among the morphological groups (H = 133.05; df = 4; P < 0.001; Figure 5). The *C. zenithicus* group had fewer gillrakers than all other cisco groups (all Dunn's Q > 5.05; all P < 0.05). Lacustrine *C. artedi* had more gillrakers than the adfluvial *C. artedi* (Dunn's Q = 3.69; P < 0.05).

Life history—Age structure differed among the five cisco morphological groups (H = 178.25; df = 4; P < 0.001). Adfluvial *C. artedi* was most divergent among the morphs having a narrow age distribution (range = 2–9 y; median = 4 y). By comparison, the other morphs had broader age distributions and were long-lived: lacustrine *C. artedi* (range = 1–33 y; median = 6 y); *C. zenithicus* (range = 2–22 y; median = 7 y); big-eye cisco (range = 3–20 y; median = 8 y); and

C. sardinella (range = 3–26 y; median = 10.5 y). The median age of adfluvial *C. artedi* was lower than the median age for all other ciscoes (all $Q > 4.50$; all $P < 0.05$).

Separate growth models for each morph best fit the length at age data (AIC = 4825; Table 4); the other models (i.e., *Common*, *Common L∞*, and *Common K*) were not supported (all ΔAIC >>>2; Burnham and Anderson 2002). von Bertalanffy growth model parameters varied among the five morphs ($F_{8,499}$ = 57.29; $P < 0.001$; Tables 4 & 5; Figure 6). The two morphs that grew the fastest, adfluvial *C. artedi* (ω = 112.40 mm · y^{-1}) and big-eye cisco (ω = 54.34 mm · y^{-1}), had the lowest average asymptotic size among the morphs (170.33 and 164.68 mm, respectively). Lacustrine *C. artedi* grew the slowest to the largest average asymptotic mean size. *C. zenithicus* expressed a nearly 14-fold faster growth rate than lacustrine *C. artedi*, its closest morphological variant.

Instantaneous total mortality (Z) differed among adfluvial and lacustrine *C. artedi* morphs, and *C. zenithicus* (F = 41.67; $P < 0.001$). Survival was low for adfluvial *C. artedi* (35%) and high for lacustrine *C. artedi* (95%) and *C. zenithicus* (86%; Figure 7). Model fit was good for adfluvial *C. artedi* (R^2 = 0.92), moderate for *C. zenithicus* (R^2 = 0.62), and poor for lacustrine *C. artedi* (R^2 = 0.19), probably due to high variation and a long lifespan of the latter group.

Physical resource use—Depth of capture differed among morphs (H = 455.65; $P < 0.001$) with adfluvial *C. artedi* occupying the shallowest water (i.e., caught in rivers during their spawning migration). Lacustrine *C. artedi* (median depth of capture = 54 m), big-eye cisco (median depth of capture = 61 m) and *C. zenithicus* (median depth of capture = 48.5 m) were all caught in waters deeper than *C. sardinella* (median = 24 m; all $P < 0.05$). The CPUE differed among morphs within the 30–59 and 60–89 m depth strata (all $P < 0.04$), but not in the shallow stratum (0–29 m) or the deep stratum (> 90 m). Lacustrine *C. artedi* and *C. sardinella* had higher CPUE in the 30–59 m depth stratum and *C. zenithicus* had higher CPUE in the 60–89 m depth stratum.

Percent buoyancy varied among morphs (H = 119.74; $P < 0.001$) with adfluvial *C. artedi* being heavier (i.e., less buoyant) than the other morphs except *C. sardinella* (all $P < 0.05$). *C. sardinella* was also heavier than *C. zenithicus*, but the other morphs did not differ in percent buoyancy.

DISCUSSION

Previous efforts to resolve coregonine cisco taxonomy in Great Slave Lake have been inconclusive due to small sample sizes, limited spatial coverage of investigation, poor condition of preserved collections, and a limited scope of analysis (Clarke 1973; Dymond 1943; Murray 2006). Taxonomic distinctions were also probably confounded by the considerable variation and plasticity in character traits observed among Great Slave Lake ciscoes.

A multivariate approach to analyzing levels of variation in morphology, meristics, age, growth, life history, and habitat use, allowed us to describe ecological groups of ciscoes that generally reflected existing coregonine taxonomy (Scott and Crossman 1973). At a minimum, our analysis supports the hypothesis that the Great Slave Lake ciscoes include two strongly differentiated species (*C. artedi* and *C. sardinella*) and an adfluvial *C. artedi* morph that is distinct from its lacustrine conspecific in terms of life history, morphology, age, growth, and mortality. *C. sardinella* has previously been identified from Great Slave Lake (Turgeon and Bernatchez 2003), but herein we provide the first comprehensive description of this species in the lake and confirm a significant range extension for the species (McPhail and Lindsey 1970). The lacustrine *C. artedi* differs little from descriptions throughout its range. In addition to these three ciscoes, linear phenotypic traits, gillraker number and morphology, and growth data support the possible

occurrence of two other, less-distinct morphs, the big-eye cisco *C. artedi* and *C. zenithicus*. Although the big-eye morph was not identified by the statistical models, it could be discriminated visually on the basis of differences in linear phenotypic traits, such as eye diameter, paired fin lengths, and head and gillraker morphology (expressed as thousands of standard length; see Table 6). In addition, the big-eye morph showed different age and growth structure compared to the other lacustrine cisco morphs. The *C. zenithicus* morph was distinguished visually and by the statistical model of linear phenotypic traits as well as by gillraker number and morphology, which were within the range for the species across its distribution (Scott and Crossman 1973). The proceeding sections of the manuscript provide a detailed description of each Great Slave Lake cisco morph within the context of existing taxonomy for North American coregonines.

Adfluvial cisco—The adfluvial cisco is strikingly uniform in appearance with little variation among individuals. This morph is characterized by its small size (maximum = 192 mm), young maximum age (9 y), young age at maturity, rapid growth, high mortality, relatively short fins with a yellow hue, long caudal peduncle, relatively short snout, and a terminal jaw (Muir et al. 2011).

Populations of *C. artedi* occur throughout the Arctic (Bernatchez and Dodson 1990; Morin et al. 1981) and have been described as anadromous, but may be amphidromous (i.e., travelling between fresh- and saltwater, but for feeding rather than breeding), but few adfluvial populations have been described, especially in North America. Blackie et al. (2012) recently showed that adfluvial cisco occur in at least three Great Slave Lake tributary rivers (i.e., Stark, Beaulieu, and Yellowknife). These authors presented differences in body and gillraker morphology between lacustrine and adfluvial cisco, consistent with those reported herein, and explored possible evolutionary scenarios for the occurrence of the two life history types.

A large population of *C. artedi* spawns in the St. Marys River, the connecting channel between lakes Superior and Huron; however, the extent to which these fish use the lake habitat is currently unknown (M.P. Ebener, Chippewa Ottawa Resource Authority, Sault Ste. Marie, Michigan, pers. comm., 2011). Fielder (2000) reported evidence from the St. Marys River of an apparent upriver progression in female CPUE by week concurrent with an increase in gonodasomatic index suggesting that these fish had migrated from the lake for spawning. It is probable that other adfluvial cisco populations occurred historically in the Laurentian Great Lakes (Christie 1974; Lawrie and Rahrer 1973). Accumulations of milling wastes from the lumber industries of lakes Huron, Michigan, and Superior during the last century have been implicated in the destruction of *C. artedi* and *C. clupeaformis* spawning grounds in many rivers and areas adjacent to the mouths of those rivers (Christie 1974) demonstrating that the adfluvial life history type is susceptible to habitat disturbances. Two eastern examples of adfluvial life history types are *C. autumnalis migratorius* (Georgi), which occur in Lake Baikal and *Coregonus peled*, which occur throughout Siberia (Berg 1948).

With the exception of the St. Marys River population, little is known about the distribution, or biological and ecological characteristics of adfluvial ciscoes in North America. In Great Slave Lake, spawning migrations of adfluvial cisco are subject to intense subsistence dipnet fisheries in some rivers, including the Yellowknife River, and the effects of these fisheries on population dynamics are unknown. Data presented herein show that fishery-induced mortality is relatively high and survival is only 35%. This raises a major conservation concern. In addition, mining operations and hydroelectric developments (e.g., Bluefish Hydro Dam replacement; Northwest Territories Power Corporation 2010) have the potential for adverse effects on adfluvial cisco populations. The adfluvial cisco is a key horizontal vector of energy transfer between Great Slave Lake, its inflowing rivers, and its connecting inland lakes. Conserving adfluvial cisco populations is a high priority of Fisheries and Oceans Canada (D. Leonard, Fisheries and Oceans Canada, Yellowknife, Northwest Territories, pers. comm., 2011).

Lacustrine Cisco—The lacustrine *C. artedi* of Great Slave Lake are similar in gross morphology, ecology, and biology to populations throughout the range. Cisco *C. artedi*, formerly known as lake herring, are the most widely distributed and most studied of the ciscoes. The literature on *C. artedi* is extensive and need not be repeated here. For data on the species see Koelz (1929), Dymond and Pritchard (1930), Pritchard (1931), Dymond (1943), McPhail and Lindsey (1970), Scott and Crossman (1973) who provided detailed accounts of the taxonomy, distribution, morphology, biology, and ecology of *C. artedi*. This species is an important prey fish and has supported subsistence and commercial fisheries throughout its range. McPhail and Lindsey (1970) and Scott and Crossman (1973) referred to *C. artedi* as a complex because of the marked phenotypic and life history variation throughout its distribution. The ranges of morphometric and meristic traits for the Great Slave lacustrine *C. artedi* fell within those reported for the taxon, but were the widest among the Great Slave Lake ciscoes.

Big-eye Cisco—Although the big-eye cisco morph was not easily discriminated by statistical models, it was visually distinct on the basis of differences in linear phenotypic traits, such as eye diameter, paired fin lengths, and head and gillraker morphology (expressed as thousands of standard length; see Table 6). Big-eye cisco can be characterized by their small body size (maximum = 204 mm), rapid growth, large eye, long, narrow dorsal fin, and darkly pigmented scales. The taxonomic affinity of the big-eye cisco remains uncertain, but it could either be a fast-growing deepwater morphological variant of *C. artedi*, or alternatively, could be a commonly occurring hybrid. Turgeon (2000) reported that ciscoes from Great Slave Lake with 40–46 gillrakers had mtDNA and nuclear alleles characteristic of *C. sardinella* whereas those that had 49–59 gillrakers had mtDNA and nuclear alleles characteristic of *C. artedi*. Two out of 63 (i.e., 3.17%) individuals with low gillraker numbers (41 and 46) possessed nuclear alleles unique to both *C. artedi* and *C. sardinella* at three loci providing evidence of hybrids between these species (Turgeon 2000). If big-eye is indeed a hybrid, it must commonly occur because it represented about 5% of our sample.

Least Cisco—*C. sardinella* in Great Slave Lake attain a moderate size (maximum = 298 mm STL and 255 g) and can be easily identified by its appearance. This species is characterized by a relatively large eye (but not as big as the big-eye), which often extends beyond the dorsal body margin, narrow interorbital width, low premaxillary angle, superior mouth orientation, extended lower jaw, long pelvic and dorsal fins, but short dorsal base, > 12 anal fin rays (all other ciscoes had < 12 anal rays), a long anal fin base, and heavy black pigmentation, especially on the ventral fins (Muir et al. 2011). *C. sardinella* was also captured in greater numbers in shallower water than the other morphs.

Uncertainties about the occurrence of *C. sardinella* in Great Slave Lake date to the early descriptions of northwestern coregonines. Bean (1889) described a new species *Coregonus pusillus* from Alaska and the Mackenzie River delta; however, Berg (1932) described Siberian *C. sardinella* as nearly identical to *C. pusillus* and both Dymond (1943) and Berg (1948) considered the two species synonymous. The *C. pusillus* type (USNM 38366) had 88 lateral-line scales, 49 gillrakers, and 14 rays in the anal fin. The number of gillrakers on the type exceeded the upper range of the Great Slave Lake *C. sardinella* specimens (Table 4); however, anadromous coregonines typically have more gillrakers than their freshwater counterparts (Scott and Crossman 1973). The high number of anal rays in *C. pusillus* was consistent with our finding that the number of anal rays in *C. sardinella* was greater by as many as 2 rays, and the anal fin base (ANL) greatly exceeded that of the other Great Slave Lake ciscoes. The fins of *C. pusillus* were also reported as dark, especially toward the distal ends, and the ventral fins were quite black. This fin pigmentation pattern is a key characteristic of *C. sardinella* in Great Slave Lake (Muir et al. 2011) and distinctly separated it from all other ciscoes in the lake, which have weakly pigmented or have immaculate fins. In general, the morphometric data given for

C. pusillus by Dymond (1943) are consistent with those for *C. sardinella* from Great Slave Lake (current study and Murray 2006). Moreover, genetic data previously showed *C. sardinella* DNA in Great Slave Lake (Turgeon and Bernatchez 2003) and recent analyses confirm that the specimens described herein belong to *C. sardinella* (AFLP; J. Turgeon, Université Laval, pers. comm.).

The Siberian *C. sardinella* are typically fluvial, inhabiting rivers, but some populations concentrate in the freshened portions of the sea, and from there migrate up the rivers for spawning (Berg 1948). Migratory and non-migratory *C. sardinella* occur across northern North America with amphidromous river- and lake-spawning life history types (Brown et al. 2007, McPhail and Lindsey 1970). The North American amphidromous form has a gillraker range of 48–53, whereas, the freshwater form ranges from 41–47 (Scott and Crossman 1973), consistent with the range for the specimens in the current study (41–46). Although we did not confirm lacustrine spawning grounds, no *C. sardinella* were caught in extensive sampling in the Yellowknife, Beaulieu, or Stark rivers flowing into Great Slave Lake (Blackie et al. 2012; A. Muir and P. Vecsei pers. observations).

Shortjaw Cisco—Great Slave Lake Shortjaw Cisco can be characterized by an included lower jaw, high premaxillary angle, downward projecting mouth, and tan dorsum colouration in fresh specimens. *C. zenithicus* is known to show considerable morphological variation across its range (Dymond 1943; Koelz 1929; Rawson 1951; Todd and Steinhilber 2002); however, the Great Slave Lake specimens collected in the current study fall within and close to the mean values reported for the species. The total range of gillraker number for *C. zenithicus* in the Laurentian Great Lakes was 32–46 (Koelz 1929), almost identical to the range we observed for the species in Great Slave Lake (33–46).

Dymond (1943), Rawson (1947), Clarke (1973), and Todd and Steinhilber (2002) considered *C. zenithicus* to occur in Great Slave Lake, but recent collections from the main basin of the lake led Murray and Reist (2003) to conclude that on the basis of gross morphology, specimens were more similar to *C. artedi* than *C. zenithicus*. Dymond (1943) concluded that the type specimen from Great Slave Lake described by Harper and Nichols (1919) as *Leucichthys macrognathus* was synonymous with *C. zenithicus*. Dymond's measurements showed the type *L. macrognathus* had the following morphological characteristics: STL 201, LLS 65, TGR 37, HLL 239, HDD 149, EYE 57, POL 62, IOW 50, MXL 90, BDD 219, CPL 129, CPD 67, DOH 195, DOL 114, ANL 107, PCL 216, and PVL 179. Most of these measures are consistent and some are close to the mean values for *C. zenithicus* in our collections (Tables 4 and 5).

Although our statistical models of body shape did not discriminate the shortjaw morph from the other Great Slave Lake ciscoes, they were reasonably well discriminated (~65% of individuals) by a model of linear phenotypic traits. Consistent with Laurentian Great Lakes specimens, low numbers of short gillrakers and a slightly shorter lower jaw than upper jaw were distinguishing traits. The shortjaw morph also had a nearly 15 times faster growth rate and an asymptotic average length that was 37% shorter compared to its closest morphological variant—lacustrine *C. artedi*.

Management implications—Ciscoes play a key role in nutrient cycling by functioning as horizontal and vertical vectors of energy transfer from primary and secondary production to their predators. Ciscoes are also important forage for top predators such as Lake Trout *Salvelinus namaycush* and Burbot *Lota lota* (Gamble et al. 2011; Ray et al. 2007; Scott and Crossman 1973).

The North American ciscoes do not easily fit into the current framework for resource management, which is broadly based on the concept of the '*biological species*'. The ciscoes typically form complexes that show ecological and morphological variation that can be both

genetically- and environmentally-based. In an extensive mitochondrial and microsatellite survey of North American cisco phylogeography, Turgeon and Bernatchez (2003) reported that the taxonomy of the *C. artedi* complex better reflected geography than evolutionary history. These authors found that *C. zenithicus* was genetically more similar to sympatric or nearby *C. artedi* than to *C. zenithicus* from other drainages, indicative of multiple independent origins of morphs. Turgeon and Bernatchez (2003) argued that *C. artedi* should be recognized as the sole legitimate taxon for North American ciscoes and that unique ecomorphotypes be recognized as evolutionary significant units (ESUs).

Identifying, characterizing, and managing locally-adapted cisco morphs that reflect important ecological and bioenergetic linkages is critical to conserving the ecological integrity of northern ecosystems. The later approach has been embraced by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). The *Species at Risk Act* (SARA) defines a *"wildlife species"* as a *"species, subspecies, variety or geographically or genetically distinct population of animal, plant or other organism, other than a bacterium or virus"* (Government of Canada 2003). This definition explicitly recognizes the importance of ecologically distinct phenotypes, and therefore, provides protection and status for cisco morphs in Canada. We support the recommendation of Turgeon and Bernatchez (2003)—*"ciscoes from lakes with distinct ecomorphotypes are recognized as ESUs, as well as each of sympatric forms when they are genetically differentiated. We recommend that an ESU strategy focusing at a very local level be adopted for continental ciscoes as a valid alternative to protect significant evolutionary processes of divergence encountered in polytypic species of newly colonized habitats."*

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Table 1. Locations, depth stratum sampled, and numbers (n) of cisco collected from Great Slave Lake.

Site	Basin	MM/DD/YY	Depth Stratum	Latitude (deg min sec N)	Longitude (deg min sec W)	n
Mackenzie Channel	Yellowknife Bay	8/24/2009	0-29	62.20.629	114.19.187	111
Tartan Rapids		9/27/2008	0-29	62.33.530	114.13.100	50
		10/1/2008	0-29	62.33.530	114.13.100	100
Sub Island North		10/4/2008	30-59	62.21.961	114.21.116	13
		10/4/2008	30-59	62.21.961	114.21.116	14
		10/17/2008	30-59	62.21.961	114.21.116	31
Sub Islands South		10/4/2008	30-59	62.21.419	114.21.957	64
		10/9/2008	30-59	62.21.419	114.21.957	10
		8/24/2009	30-59	62.21.419	114.21.957	50
		9/25/2009	30-59	62.21.419	114.21.957	7
Negus Point		10/17/2008	0-29	62.25.475	114.21.030	7
		10/18/2008	0-29	62.25.475	114.21.030	24
Beaulieu River	East Arm	10/14/2008	0-29	62.20.792	113.11.487	75
Christie Bay		10/16/2008	30-59	62.29.053	111.11.790	12
		10/16/2008	60-89	62.29.053	111.11.790	11
		10/16/2008	> 90	62.29.053	111.11.790	24
		10/17/2008	60-89	62.29.053	111.11.790	23
		10/17/2008	30-59	62.29.053	111.11.790	26
Red Cliff Bluffs		10/15/2008	30-59	62.21.388	111.40.776	24
		10/15/2008	>90	62.21.388	111.40.776	18
Outer East Arm		10/14/2008	>90	61.59.448	113.92.881	0

Table 2. Linear morphometric measures for cisco; modified from Koelz (1929), Scott (1960) and Vuorinen et al. (1993).

Character	Acronym	Definition
Fork Length	FRL	• tip of premaxilla to the caudal fork with the fin open
Standard length	STL	• tip of the premaxilla to the caudal flexure (crease created when tail is flexed)
Preobital length	POL	• tip of the premaxilla to the anterior fleshy margin of the orbit
Orbital length	OOL	• distance between anterior and posterior fleshy margins of the orbit
Post orbital length	PSL	• posterior fleshy margin of the orbit to posterior bony margin of the operculum
Trunk length	TTL	• distance along the horizontal body axis between the posterior margin of the operculum and the origin of the dorsal fin
Dorsal length	DOL	• origin of dorsal fin to the posterior edge of the fin behind the final ray
Dorsal height	DOH	• origin of dorsal fin to the tip of the longest ray
Lumbar length	LUL	• distance along the horizontal body axis between the end of the dorsal fin and the origin of the anal fin
Anal length	ANL	• distance along the horizontal body axis between the origin and the posterior edge of the fin
Caudal peduncle length	CPL	• distance along the horizontal axis of the body between the posterior of the anal fin and the caudal flexure
Head depth	HDD	• vertical distance through the pupil of the eye from the dorsal surface of the cranium to the ventral edge of the gular region
Head length	HLL	• sum of preorbital, orbital, and post orbital lengths
Body depth	BDD	• vertical distance from the dorsal origin to the ventral surface of the body
Caudal peduncle depth	CPD	• the least vertical depth of the caudal peduncle
Interorbital width	IOW	• shortest distance of bone between the upper rims of the orbits
Maxillary length	MXL	• anterior point of premaxillae to posterior end of the maxilla
Maxillary width	MXW	• greatest width along the maxillary
Pectoral fin length	PCL	• extreme base of outermost ray to farthest tip of fin
Pelvic fin length	PVL	• extreme base of outermost ray to farthest tip of fin
Adipose length	ADL	• distance from the point where skin and scales meet at the anterior end of the fin to the free posterior margin of the fin
Middle gillraker length	GRL	• length of the gillraker on the ceratobranchial-epibranchial joint on the first arch; taken from the left side of fish
Lower arch length	LAL	• length from the start of the lower arch to the base of the middle gillraker; taken from left side of fish
Premaxillary angle	PMA	• angle between the horizontal axis of the head and the premaxillae

Table 3. Meristic characters for cisco; modified from Koelz (1929) and Vourinen et al. (1993).

Character	Acronym	Definition
Dorsal rays	DRC	• all rays in the dorsal fin including rudimentary rays; anterior fin rays were excluded from counts unless they were 2/3 the length of the longest ray; when the shortest ray was split at the base, it was counted as a single ray (for all ray counts)
Anal rays	ARC	• all rays in the anal fin including rudimentary rays
Pectoral rays	PRC	• all rays in the left pectoral fin counted
Pelvic rays	VRC	• all rays in the left pelvic fin counted
Upper gillrakers	UGR	• number of gillrakers, including all rudiments, on the first, left epibranchial including the raker on the ceratobranchial-epibranchial joint
Lower gillrakers	LGR	• number of gillrakers, including all rudiments, on the first, left ceratobranchial
Suprapelvic scales	SPS	• a single column of scales enumerated from the axillary process to the lateral line
Scales above the lateral line	ULS	• a single column of scales enumerated from the origin of the dorsal fin to the lateral line
Lateral line scales	LLS	• first pored scale touching the pectoral girdle to last scale of the body on lateral line. If scales are missing, pockets from scales are to be counted instead

Table 4. Results from four nested von Bertalanffy models fit to length-at-age data for Great Slave Lake ciscoes: 1) General: separate parameter estimates for each morph; 2) Common L_∞: constant L_∞ among morphs, but varying K; 3) Common K: constant K, but varying L_∞; and 4) Common: the same parameter estimates for all morphs combined. The "best" model was selected by Akaike information criterion (AIC); ΔAIC = AIC difference between a candidate model and the General model.

Model	RSS	DF	MS	F	P	AIC	ΔAIC
General	373651	499	748	57.29	<0.001	4825	—
Common L_∞	483505	503	961	60.70	<0.001	4948	123
Common K	508530	503	1011	51.52	<0.001	4974	149
Common	716880	507	1414	30.34	<0.001	5140	315

Table 5. von Bertalanffy growth model parameter estimates for cisco species or morphs and the common model fit to all Great Slave Lake, NT cisco morphs combined. L_∞ is the asymptotic average length (mm); and K is the growth coefficient (y^{-1}). Annual growth rate (ω) was estimated by $L_\infty * K$ ($mm \cdot y^{-1}$; Gallucci and Quinn 1979).

Species or Morph	L_∞	K	ω	SS_{resid}	DF
Adfluvial *C. artedi*	170.30 ± 3.03	0.66 ± 0.05	112.40	29909	223
Lacustrine *C. artedi*	384.70 ± 16.44	0.01 ± 0.01	3.85	220929	151
Big-eye *C. artedi*	164.68 ± 5.01	0.33 ± 0.04	54.34	8367	32
C. sardinella	238.69 ± 25.21	0.15 ± 0.04	35.80	7111	7
C. zenithicus	243.16 ± 10.58	0.22 ± 0.03	53.50	107336	85
Common Model	270.90 ± 5.96	0.18 ± 0.01	48.76	716880	507

Table 6. Mean proportionate measurements of body parts of Great Slave Lake coregonine ciscoes expressed in thousandths of the standard length (STL; mm) ± standard error; raw data are given in parentheses.

Variable	Adfluvial C. artedi	Lacustrine C. artedi	Big-eye cisco C. artedi	C. sardinella	C. zenithicus
STL*	157.79 ± 0.83	200.83 ± 5.13	146.06 ± 3.72	225.83 ± 7.02	185.36 ± 3.95
TTL	263.37 ± 0.93	257.24 ± 1.19	260.46 ± 2.43	244.38 ± 2.42	260.95 ± 1.88
	(41.60 ± 0.29)	(51.56 ± 1.33)	(38.06 ± 1.06)	(55.12 ± 1.87)	(48.55 ± 1.19)
DOL	105.50 ± 0.47	112.22 ± 0.66	105.29 ± 1.05	103.90 ± 1.2	110.77 ± 0.86
	(16.66 ± 0.12)	(22.97 ± 0.71)	(15.40 ± 0.46)	(23.26 ± 0.69)	(20.65 ± 0.5)
DOH	175.55 ± 0.76	191.64 ± 1.37	200.59 ± 2.39	201.97 ± 2.14	191.73 ± 1.47
	(27.68 ± 0.17)	(38.23 ± 0.89)	(29.19 ± 0.73)	(45.29 ± 1.36)	(35.26 ± 0.69)
LUL	184.55 ± 1.15	181.05 ± 1.3	170.93 ± 3.21	193.39 ± 2.27	177.87 ± 1.34
	(29.09 ± 0.22)	(36.58 ± 1.03)	(24.97 ± 0.8)	(43.69 ± 1.55)	(32.94 ± 0.74)
ANL	104.82 ± 0.64	108.39 ± 0.9	105.10 ± 1.66	122.68 ± 1.28	107.40 ± 0.88
	(16.55 ± 0.14)	(21.87 ± 0.61)	(15.36 ± 0.48)	(27.76 ± 0.99)	(19.98 ± 0.47)
CPL**	131.98 ± 0.9	117.27 ± 0.9	115.53 ± 2.07	121.68 ± 1.86	122.27 ± 1.19
	(20.79 ± 0.16)	(23.66 ± 0.66)	(16.84 ± 0.53)	(27.50 ± 1.03)	(22.76 ± 0.58)
BDD	208.48 ± 0.93	223.35 ± 2.06	218.57 ± 3.47	199.91 ± 2.51	218.01 ± 2.36
	(32.91 ± 0.23)	(46.76 ± 1.7)	(32.05 ± 1.13)	(45.19 ± 1.6)	(40.91 ± 1.15)
CPD	73.14 ± 0.25	72.82 ± 0.44	71.77 ± 0.83	78.51 ± 0.82	73.05 ± 0.66
	(11.53 ± 0.06)	(14.94 ± 0.47)	(10.48 ± 0.31)	(17.76 ± 0.62)	(13.60 ± 0.35)
PCL	170.17 ± 0.68	178.08 ± 1.59	187.00 ± 2.77	187.04 ± 2	172.56 ± 1.49
	(26.78 ± 0.12)	(35.30 ± 0.85)	(27.16 ± 0.64)	(41.88 ± 1.23)	(31.85 ± 0.69)
PVL	165.77 ± 0.65	174.74 ± 1.27	185.99 ± 2.38	185.32 ± 1.91	171.52 ± 1.33
	(26.12 ± 0.14)	(34.65 ± 0.82)	(27.00 ± 0.59)	(41.44 ± 1.17)	(31.59 ± 0.64)
ADL	60.53 ± 0.4	68.05 ± 0.61	66.91 ± 0.96	69.83 ± 1.08	68.40 ± 0.75
	(9.55 ± 0.08)	(13.90 ± 0.42)	(9.76 ± 0.28)	(15.70 ± 0.53)	(12.75 ± 0.32)
POL	52.46 ± 0.34	57.43 ± 0.47	60.93 ± 1.2	45.57 ± 0.94	56.41 ± 0.55

Variable	Adfluvial *C. artedi*	Lacustrine *C. artedi*	Big-eye cisco *C. artedi*	*C. sardinella*	*C. zenithicus*
	(8.26 ± 0.06)	(11.66 ± 0.36)	(8.82 ± 0.2)	(10.13 ± 0.29)	(10.38 ± 0.22)
OOL**	65.19 ± 0.36	60.64 ± 0.53	75.22 ± 0.85	64.99 ± 0.97	63.41 ± 0.6
	(10.24 ± 0.04)	(11.80 ± 0.24)	(10.98 ± 0.3)	(14.44 ± 0.36)	(11.56 ± 0.2)
PSL**	111.32 ± 0.33	115.05 ± 0.56	114.59 ± 1.03	100.44 ± 0.9	115.05 ± 0.59
	(17.55 ± 0.09)	(23.37 ± 0.68)	(16.72 ± 0.45)	(22.53 ± 0.67)	(21.34 ± 0.47)
HLL	228.97 ± 0.72	233.12 ± 1.02	250.73 ± 1.91	211.01 ± 2.3	234.88 ± 1.19
	(36.05 ± 0.15)	(46.83 ± 1.25)	(36.52 ± 0.87)	(47.10 ± 1.27)	(43.28 ± 0.86)
HDD	104.92 ± 0.51	105.76 ± 0.5	117.28 ± 1.13	96.21 ± 1.07	107.80 ± 0.64
	(16.52 ± 0.09)	(21.33 ± 0.59)	(17.09 ± 0.42)	(21.46 ± 0.57)	(19.91 ± 0.43)
IOW**	53.69 ± 0.33	54.58 ± 0.49	53.94 ± 0.95	44.51 ± 0.54	54.18 ± 0.59
	(8.46 ± 0.06)	(11.41 ± 0.4)	(7.94 ± 0.27)	(9.96 ± 0.3)	(10.17 ± 0.28)
MXL	77.87 ± 0.41	84.78 ± 0.57	91.60 ± 0.97	74.65 ± 0.81	83.90 ± 0.6
	(12.25 ± 0.07)	(16.98 ± 0.45)	(13.32 ± 0.31)	(16.73 ± 0.5)	(15.41 ± 0.3)
MXW	23.58 ± 0.14	22.81 ± 0.21	23.50 ± 0.39	21.78 ± 0.51	22.34 ± 0.22
	(3.71 ± 0.02)	(4.58 ± 0.13)	(3.42 ± 0.09)	(4.86 ± 0.16)	(4.13 ± 0.09)
GRL**	40.99 ± 0.23	39.51 ± 0.54	41.74 ± 1.01	34.80 ± 0.67	34.79 ± 0.43
	(6.45 ± 0.04)	(7.93 ± 0.22)	(6.06 ± 0.18)	(7.68 ± 0.31)	(6.37 ± 0.14)
LAL	93.28 ± 0.44	100.97 ± 0.67	110.71 ± 1.12	85.74 ± 1.32	102.33 ± 0.78
	(14.68 ± 0.08)	(20.49 ± 0.59)	(16.18 ± 0.51)	(18.80 ± 0.63)	(18.83 ± 0.43)

*Standard length is given as an untransformed measure;

** Traits used in secondary analysis of morphological variation (see methods).

Table 7. Mean counts of calcified body parts from Great Slave Lake coregonine ciscoes ± standard error; ranges are given in parentheses.

Variable	Adfluvial C. artedi	Lacustrine C. artedi	Big-eye cisco C. artedi	C. sardinella	C. zenithicus
TGR*	42.25 ± 0.12	43.93 ± 0.28	42.5 ± 0.37	42.84 ± 0.28	39.94 ± 0.2
	(39-46)	(36-56)	(38-48)	(41-46)	(33-46)
LLS	74.95 ± 0.25	73.44 ± 0.42	71.09 ± 1.07	77.47 ± 1.22	72.95 ± 0.5
	(67-86)	(64-84)	(61-82)	(63-83)	(65-83)
SPS	7.52 ± 0.04	7.53 ± 0.07	7.26 ± 0.1	7.21 ± 0.19	7.48 ± 0.08
	(6-9)	(6-9)	(7-8)	(6-9)	(6-9)
ULS	7.7 ± 0.04	7.84 ± 0.07	7.37 ± 0.14	8 ± 0.11	7.7 ± 0.08
	(7-9)	(6-9)	(7-9)	(7-9)	(6-9)
DRC	11.06 ± 0.04	10.97 ± 0.06	10.65 ± 0.17	10.2 ± 0.11	10.76 ± 0.08
	(9-13)	(9-14)	(9-14)	(9-12)	(9-14)
ARC	12.04 ± 0.05	11.85 ± 0.07	11.74 ± 0.14	13.18 ± 0.11	11.75 ± 0.1
	(9-14)	(10-15)	(10-14)	(12-14)	(9-15)
PRC	16.11 ± 0.06	16.05 ± 0.09	16 ± 0.17	14.81 ± 0.09	16.23 ± 0.11
	(14-19)	(12-18)	(12-18)	(14-16)	(11-18)
VRC	11.35 ± 0.03	11.29 ± 0.04	11.26 ± 0.14	11.15 ± 0.09	11.22 ± 0.07
	(10-13)	(10-15)	(9-13)	(10-12)	(9-16)
PMA	45.75 ± 0.52	43.39 ± 0.64	34.29 ± 1.43	24.03 ± 1.12	50.49 ± 0.92
	(21-72)	(23-76)	(20-59)	(15-45)	(22-76)

*Total number of gillrakers (i.e., sum of UGR and LGR)
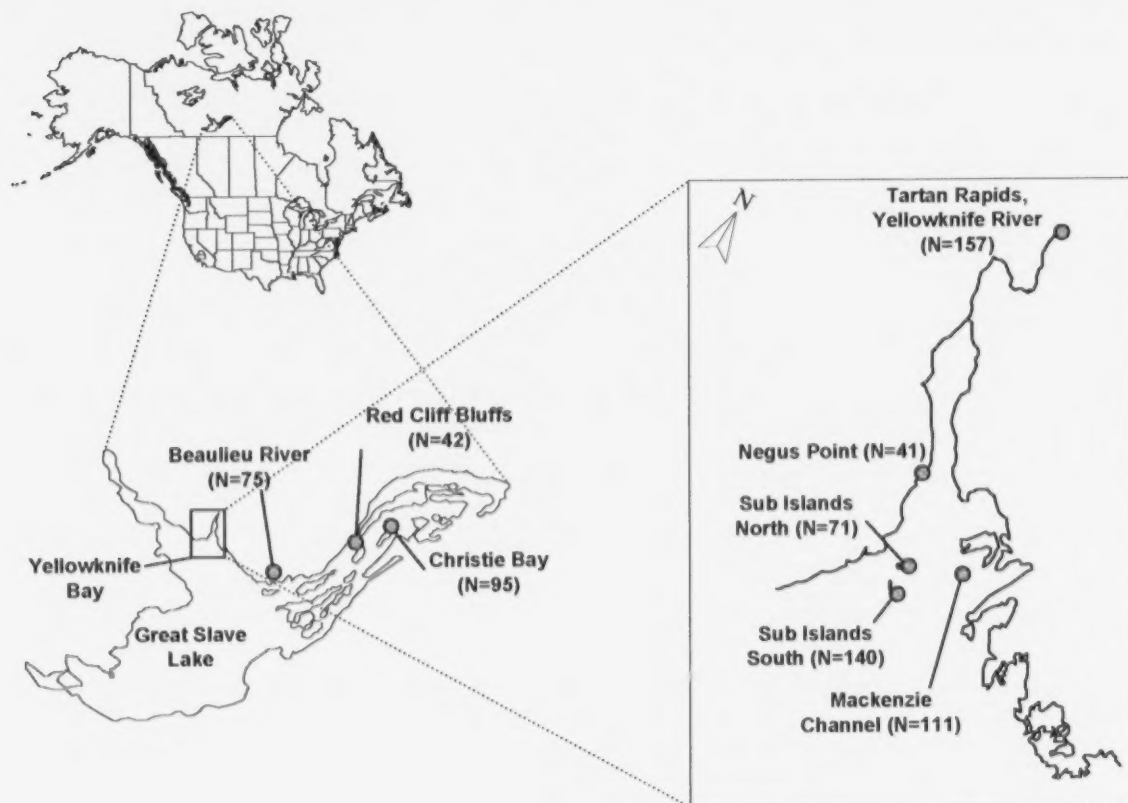
Figure 1. Cisco sampling locations in Yellowknife Bay and the east arm, Great Slave Lake, NT.
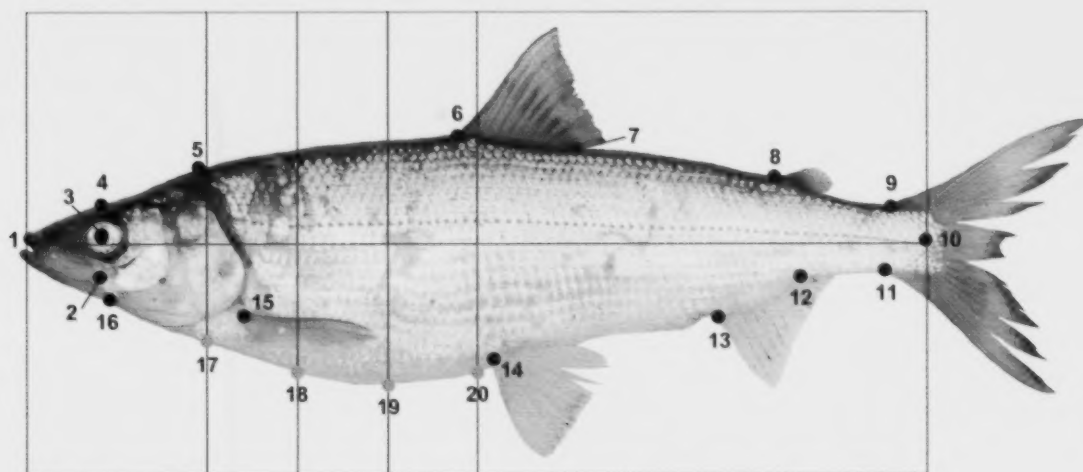
Figure 2. Landmark order and placement for digitizing body shape. Black dots (1–16) represent homologous landmarks and grey dots (17–20) represent semi-sliding landmarks that were positioned at 0.20, 0.30, 0.40, and 0.50*standard length as indicated by the grid.
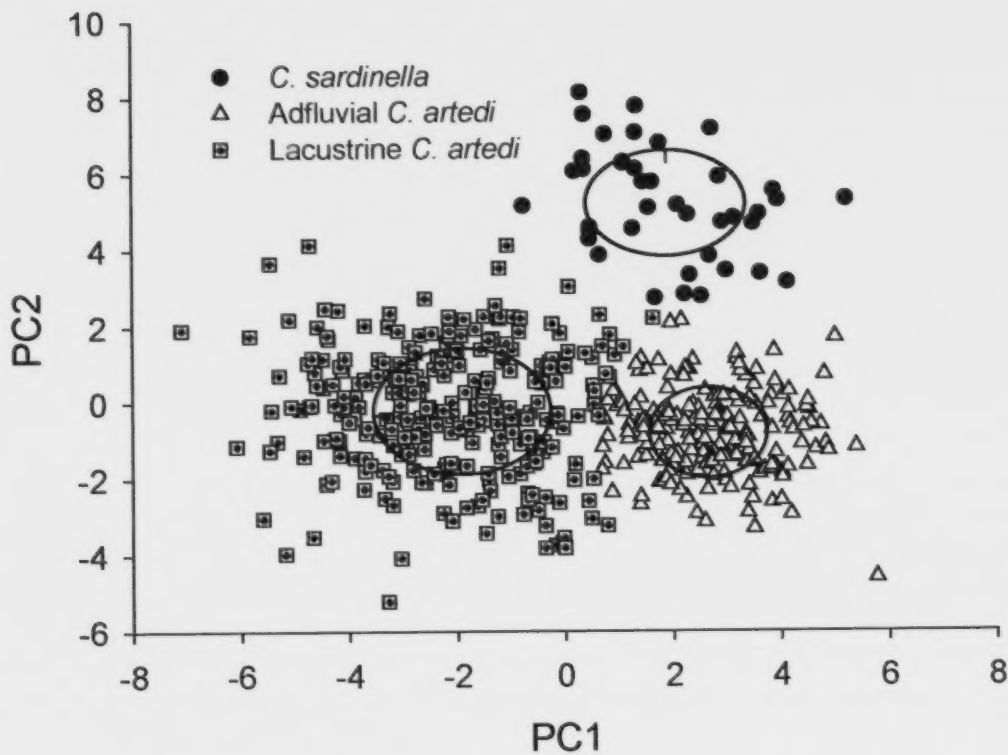
Figure 3. Ordination of principal component scores (n = 508) for 36 partial warps defining geometric body shape for coregonine ciscoes in Great Slave Lake, NT. Three groups were identified on the basis of size-independent body shape with no a priori group assignments. These three groups were compared to a priori assignments made in the field. One group (Δ) was 99% adfluvial cisco C. artedi; the second group (●) was 93% C. sardinella; the third group (▫) was a lacustrine group that consisted of a mixture of specimens field-identified as lacustrine C. artedi, a big-eye morph of C. artedi, and C. zenithicus.
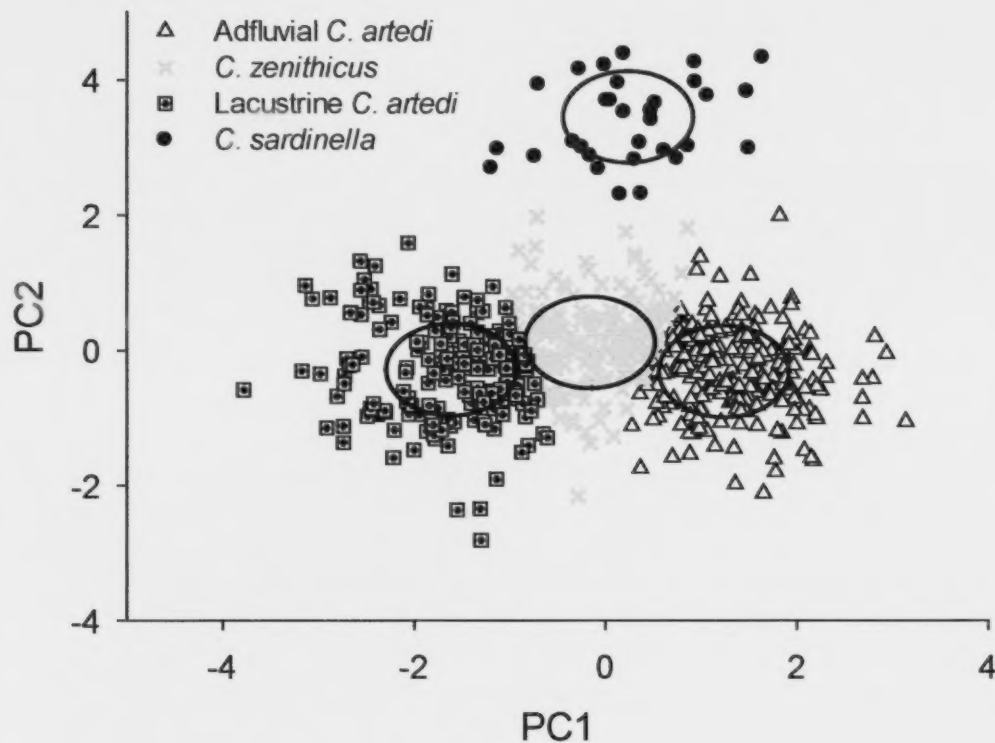
Figure 4. Ordination of principal component scores (n = 616) for size-corrected eye diameter, postorbital length, interorbital width, middle gillraker length, and caudal peduncle length for ciscoes in Great Slave Lake, NT. Four groups were identified on the basis of the linear phenotypic measures with no a priori group assignments. One group (Δ) contained 80% of the fish field-identified as adfluvial C. artedi; a second group (X) contained 65% of the fish field-identified as C. zenithicus; a third group (□) contained 77% of the fish field-identified as lacustrine C. artedi, and a fourth group (●) contained 97% of the fish identified as C. sardinella in the field. The model did not discriminate big-eye C. artedi and 97% of fish identified as big-eye in the field were grouped with the adfluvial C. artedi by the model.
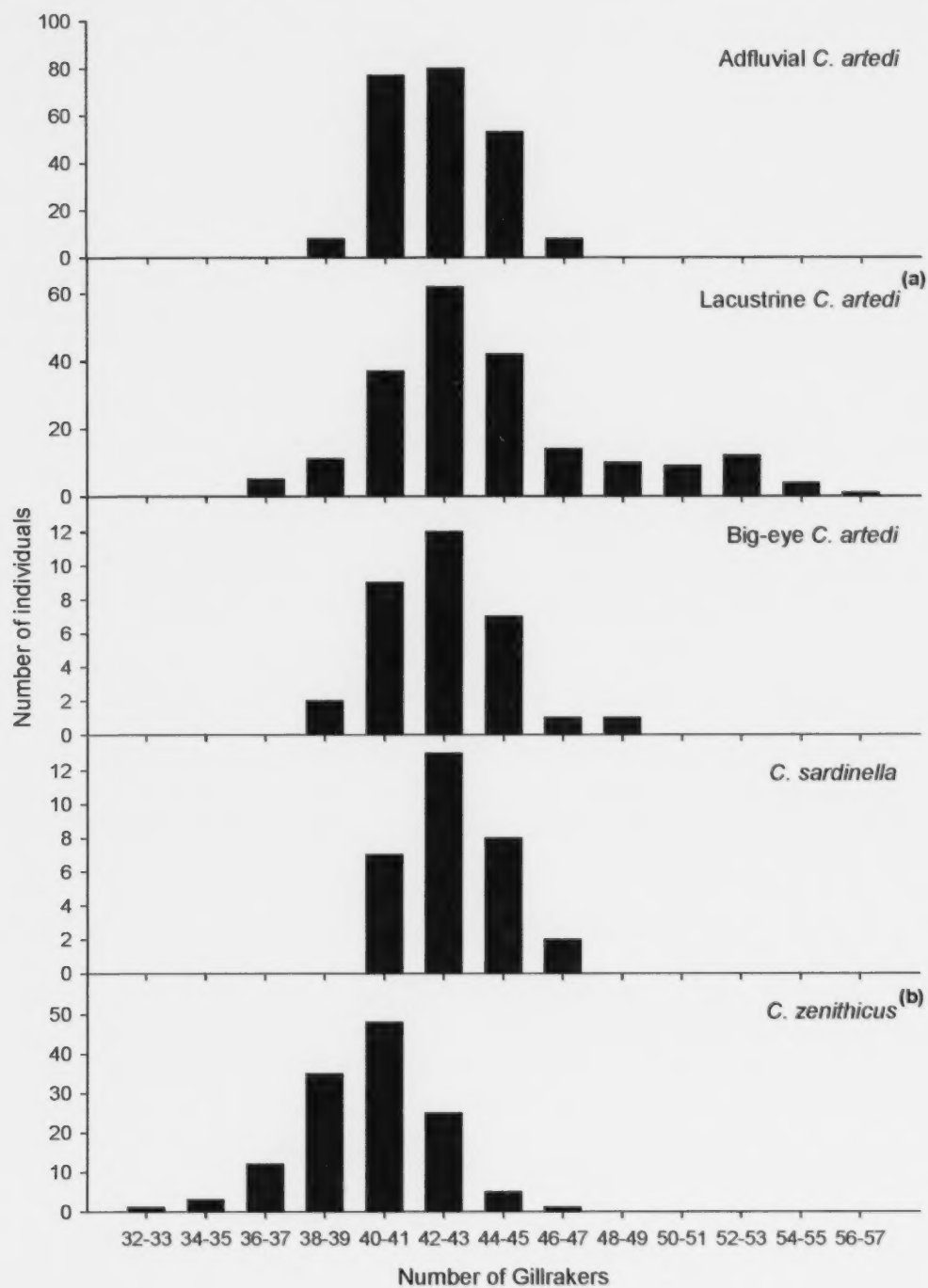
Figure 5. Gillraker frequency distributions for the five cisco morphs from Great Slave Lake, NT; (a) differs from adfluvial Coregonus artedi; (b) differs from adfluvial C. artedi, lacustrine C. artedi, big-eye C. artedi, and C. sardinella (Dunn's pairwise multiple comparisons; all P < 0.05).
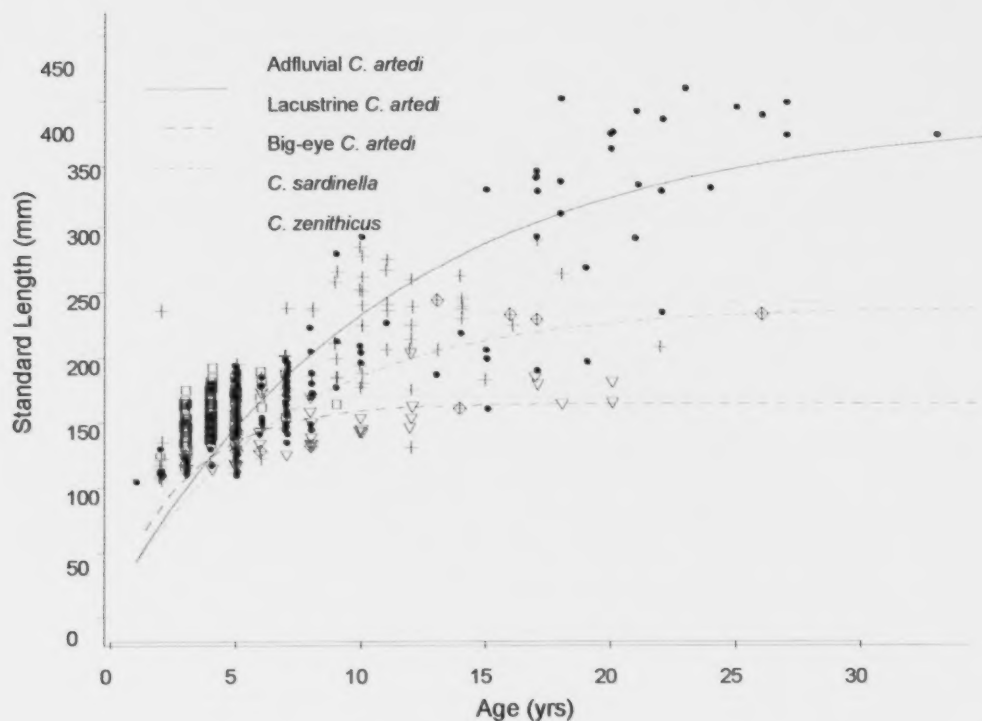
Figure 6. Growth curves for cisco morphs from Great Slave, NT generated by fitting von Bertalanffy length-age models to standard-length-at-otolith-age for the five cisco morphs. Separate growth models for each morph best fit the data. Adfluvial C. artedi ($\omega = 112.40 \ mm \cdot y^{-1}$) and big-eye cisco ($\omega = 54.34 \ mm \cdot y^{-1}$) had the fastest growth rates and the lowest average asymptotic size among the morphs (170.33 and 164.68 mm, respectively). Lacustrine C. artedi grew the slowest to the largest average asymptotic mean size. C. zenithicus expressed a nearly 14-fold faster growth rate than lacustrine C. artedi, its closest morphological variant.
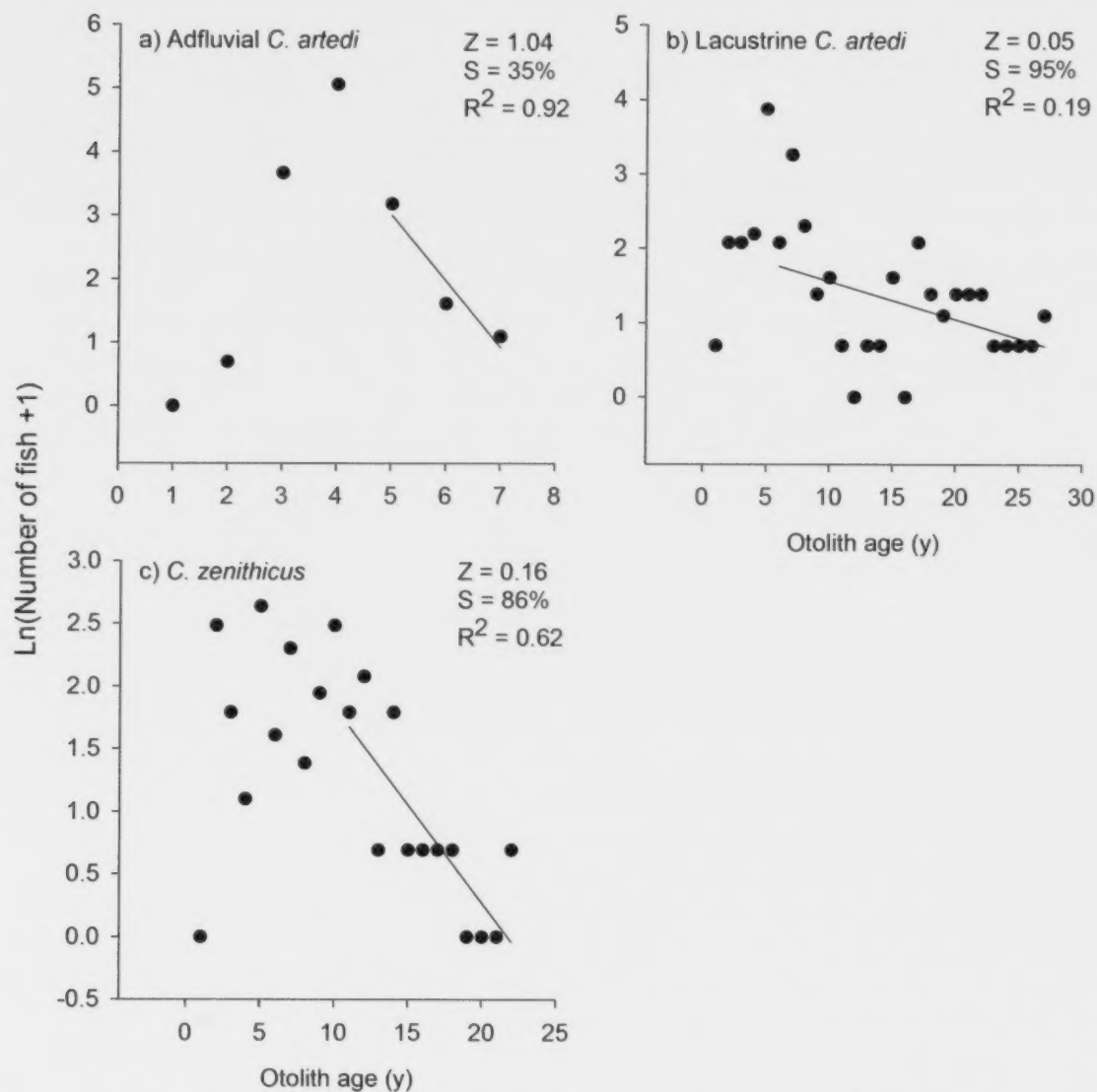
Figure 7. Age distributions enabled calculation of instantaneous total mortality (Z) for the adfluvial and lacustrine C. artedi morphs, and C. zenithicus. Survival was low for adfluvial C. artedi (35%) and high for lacustrine C. artedi (95%) and C. zenithicus (86%).

ACKNOWLEDGEMENTS